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THE PSYCHOLOGICAL BULLETIN

HABIT FORMATION AND HIGHER MENTAL PROCESSES IN THE RAT

BY W. T. HERON
University of Minnesota

This summary covers approximately the years 1928 to 1931 inclusive. It was the original intention of the reviewer to include the work on all species for this period. However, when the bibliography had been completed it was found that limitations of space would preclude such a general review. This is unfortunate as a large amount of very important and interesting work has been done on other animals, particularly the primates, during this period. It is hoped that this work may be reviewed by someone in the near future. The last general review of this nature covering all species was by Tolman (143). This summary, therefore, takes up the work where he left off except that it is confined to the rat.

I. TECHNIQUE AND APPARATUS

(a) *Learning curves.* Valentine (162) plotted the learning curve of rats and found that it makes little difference whether the hyperbola or arc cotangent function is used as far as "goodness of fit" to actual data is concerned. He states, however, that "the arc cotangent function, particularly with the addition of the S-parameter, is much more flexible than the hyperbola and is therefore more valuable in fitting learning curves."

(b) *Reliability of measuring devices.* A large amount of work has appeared during the period in question on the reliability of the maze. The majority of the studies are on some pattern of the multiple-T maze and retracings have been prevented to a certain extent by means of doors placed at critical points in the maze. Stone

and Nyswander (135) studied the reliability of the Stone multiple-T maze by four different methods. These methods and the range of coefficients from different groups of animals are as follows: (1) correlating the total errors on odd trials with total errors on even trials, .59 to .97; (2) correlating the total errors on odd numbered blind alleys with total errors on even numbered blind alleys, .71 to .96; (3) correlating the total errors for first half of maze with total for second half, .66 to .96; (4) correlating total errors for a segment of the series of trials with total errors for any other segment of the series, .46 to .97. Some correlations for time were also made and they compare favorably with those given above.

Tolman and Nyswander (141) also have made an extensive study of reliability and found the T-maze is the most reliable of any form at present in use. Their correlations for the T-maze are similar to those given above.

Stone (138) examined the reliability of the Carr maze and found it to be too low for use in research.

Heron (58) was able to verify the findings of Stone and Nyswander (135) on the Stone Multiple-T maze. However, he found that the test-retest correlations for this maze were discouragingly low.

Tryon (151) made a thorough study of the question of reliability from both the theoretical and practical standpoint. He states eight principles which should be observed in any testing situation. He then trains groups of animals in two patterns of the multiple-T type of maze and finds correlations for the errors on the odd vs. even trials to be .98 for maze X and .96 for maze Y. On the basis of these correlations he calculates the error of an individual rat's score owing to unsystematic factors and finds in X maze that any two rats whose error scores differ by 13.52 errors or more are unquestionably different from each other. He concludes that ". . . the rat maze may be so constructed as to be *even more reliable* as an instrument with which to measure individual differences in a behavior trait *than the best human mental measuring devices.*"

Tryon (154) finds correlations ranging from .81 to .88 between learning and relearning with an interval of six to eight months. Various interpolated conditions during this rest period did not markedly affect the correlations. These correlations are much higher than those obtained by Heron (58).

McNemar and Stone (113) also have studied this question. They used various intervals of rest but none as long as Tryon's and found correlations averaging .65.

Tryon (153) has also studied the correlation between scores obtained in two different mazes of the multiple-T type. He finds a correlation of approximately .8 for errors.

Corey (16) obtained high reliability coefficients for the elevated skeleton maze.

Liggett (92) found a correlation of .82 for errors in his sectional maze which involves the multiple-T principal to a certain extent.

Stone (137) studied the reliability of his multiple discrimination box and found reliability coefficients which ranged significantly lower than those which he obtained for the maze. The coefficients were somewhat higher for animals in a second training in which they had to learn to do the opposite of what they had previously learned.

(c) *New apparatus.* 1. *Maze.* Warner and Warden (174) present an analysis of all mazes which have been used in animal psychology and describe a new maze composed of units which can be changed into various patterns. Warden (167) also describes this maze. Tolman, Tryon, and Jeffress (143) describe an ingenious automatic maze. This apparatus introduces one animal at a time to the maze and automatically records its path through the maze. Miles (115) describes an elevated narrow-path maze for rats which he considers to have certain advantages over mazes of the traditional type. Hunter (69) describes a tridimensional maze and contrasts it with the bidimensional spatial maze and the temporal maze. Liggett (91, 93) and Trueblood (149) describe certain maze modifications which they have made.

The tendency has been to be more careful in maze design than formerly. Efforts have been made to make different portions of the maze more nearly equal in difficulty for animals and to use a homogeneous design throughout the whole maze rather than the heterogeneous patterns of former years.

2. *Discrimination apparatus.* Stone (137) has described a multiple discrimination box in which the animal has to make five discriminations in going through the apparatus. Lashley (81) describes a jumping procedure which he has developed as a method for the study of pattern-vision in the rat. This method establishes the habit much more quickly than former methods. Munn (121) has also attested to the value of this method.

3. *Problem boxes.* Jenkins (77) has described a problem box, the solution to which can be varied in complexity and which he believes can be successfully used with various species of animals.

4. *Motivation.* Jenkins, Warner, and Warden (76) have

described an apparatus for the study of motivation using the obstruction principle.

5. *Miscellaneous apparatus.* Drake (27) describes an apparatus to measure the acuity of the proprioceptive senses in the rat. Fritz (40) has designed an apparatus to measure reaction time, and Dunlap (28) describes a method of administering alternating current to the animal.

II. EXPERIMENTS ON DISCRIMINATING ABILITY

The reader will find a general review of visual discrimination in an article by Stagner (134).

1. *Audition.* Hunter (67) tried to train rats to make a discrimination on the basis of tone by gradually reducing the noise factor in a compound stimulus of noise and tone. The rats learned the discrimination on the basis of the compound stimulus but when the noise factor had been removed the animals showed no ability to make the correct reaction. These results, therefore, confirm Hunter's previous results on the lack of tonal sensitivity in the rat. In contradiction to the results of the series of experiments by Hunter are the results of Muenzinger (118) who obtained evidence of tonal discrimination. All of these experiments seem to have been carefully performed and the difference in findings are, for the moment, inexplicable. However, the anatomical evidence, so far as the internal ear is concerned, would seem to support the results in favor of tonal discrimination.

2. *Vision.* (a) *Discrimination of distance.* Robinson and Wever (126) present data concerning distance perception, obtained by determining the distance from a closed door that the rat would distinguish the door as closed. They found this distance to be 18 inches for albinos and 30 inches for pigmented animals.

Lashley (86) also has studied distance perception by the jumping technique (81) in animals with cerebral lesions. He does not, however, give norms, but promises a further study using an improved technique.

Yoshioka (180) by a study of the animal in a maze in which the length of the alleys could be altered came to the conclusion that Weber's law holds in the discrimination of maze distances within the limits of his experiment. The sensory field involved in this experiment is probably primarily kinaesthesia rather than vision.

(b) *Visual acuity.* Lashley (83) tested visual acuity by forcing animals to discriminate between vertical and horizontal black-white

striations. He finds the threshold for albino rats to be two to four times higher than for the pigmented animals.

(c) *Form discrimination.* Fields (34, 35, 36, 37, 38) has performed a series of experiments on form discriminations. He finds that rats can discriminate forms rather easily. Munn (119, 120, 122) has adversely criticized Fields' work both on theoretical and experimental grounds. Except from the standpoint of methodology, this discussion has largely lost its significance in view of the fact that Lashley (81, 86) has shown by his method that the rats have a rather well developed ability to make form discriminations.

Borovski (4, 5) has done some interesting experiments on the problem of the animal's ability to use a combination of visual stimuli in making a discrimination. He finds that the rats discriminate best if the cues differ in size, shape, and elevation above the floor and poorest if cues differed only in shape. He also finds that his rats did not learn to discriminate combinations of black or white and form, although either cue could be used separately. From this he concludes that the knowledge of the value of a single cue taken alone cannot be used to predict its value in combination with others.

In experiments on combined cues it is of great importance to determine whether the animal is really reacting to the combined cue or only to one element in it. This makes necessary the performance of a large number of detailed control experiments.

(d) *Brightness vision.* Slater (133) determined that rats could discriminate brightness differences as small as 32 per cent of a brighter standard. Hubbard (66) found that rats would learn more easily a brightness discrimination if they went through a lighted hole rather than in the usual fashion of the Yerkes discrimination apparatus. The reasons for this finding were not definitely established.

Fritz (41) and Rose (127) have worked upon the problem of training animals to form two antagonistic visual discrimination habits. Rose performed this experiment by the use of a double discrimination box in one part of which the animal had to respond to white as opposed to black and in the other part to black as opposed to white. The majority of his animals learned this problem with little difficulty. Fritz, on the other hand, trained the animals on first one discrimination until learning was evident and then on the other, and thus alternated the training over a long period of time. He found that each time the animals were shifted to the opposite situation they had to learn it practically as a new problem.

3. *Olfactory discrimination.* Liggett (90) has done an extensive

piece of work on olfactory sensitivity. In one part of his experiment he used Vincent's technique of laying an olfactory trail in a maze. The results of this method failed to indicate that the animals made use of the trail in learning. He found, however, that anosmic rats ran faster than normal rats. This fact in itself may indicate that olfactory cues enter into the complex of cues in the maze although they may not be used as orientational cues. For evidence in support of this point the reader is referred to the article by Buytendijk (9). In the discrimination boxes he found that some rats gave evidence of making a discrimination between some of the stimuli used. These discriminations, however, were all very unstable. In another experiment on the location of food he found that the animals were able to locate cheese when it was buried in sawdust.

In view of the anatomical data on the olfactory apparatus of the rat, it may be thought surprising that the discriminations were so hard to establish and so unstable in the discrimination boxes. It is the opinion of the reviewer, that the Yerkes discrimination apparatus and many of the T-discrimination boxes which are used violate a psychological principle in such a way that one should be surprised when the animal does form the discrimination rather than when it does not.

In order to learn the discrimination it is necessary that the animal should do one of two things or both, namely, to form an association between the positive stimulus and the reward, generally food, or to form an association between the negative stimulus and punishment. In order to form an association according to the law of contiguity it is necessary that the two stimuli should be together in time or space. While their "togetherness" need not be interpreted too literally still the further separated the two experiences are the more difficult it is for the animal to make the association. It is quite obvious that in the Yerkes box and in many T-boxes the food and the positive stimulus are quite widely separated both in time and space, therefore it is difficult for the animal to make the association between these two factors. In the Yerkes box the punishment, if an electric shock is used, and the negative stimuli are much closer together. This may be the reason that it is almost necessary to use punishment in the Yerkes box if a discrimination is to be formed in any reasonable length of time. The remedy of this defect to a certain extent in the Lashley "jumping technique" may be one factor that accounts for its effectiveness.

4. *Proprioceptive discrimination.* Ruch (128, 129) has studied

the ability of the rat to make a discrimination on what is presumably a proprioceptive basis. He used a box to which alleys are hinged in such a fashion that they could be varied from the horizontal position. In one experiment he finds that some animals may discriminate a deviation from the horizontal of 3 degrees and in another experiment some animals made the discrimination with 1 degree deviation.

It seems to the reviewer that the apparatus described by Drake (27) for this purpose has many advantages over that used by Ruch.

5. *Momentum*. Yoshioka (182) made some observations which suggest that the rat may have a "sense of momentum."

6. *Discrimination of maze patterns*. Yoshioka (177, 183) finds that rats are able to differentiate in a preferential way between mazes of different patterns but of the same total length. He is not certain what factors are responsible for the preferences shown and promises further work on this question.

III. CUES USED IN LEARNING

This problem has occupied a great deal of the attention of experimenters during the period covered by this review. That the solution of the problem is of fundamental importance for theoretical discussion and for the interpretation of results is attested by the discussion between Hunter (72, 73) and Lashley (85). This discussion will be mentioned again later.

1. *Vision*. Higginson (60) used a maze in which a door into an alley was found open by the animal only after it had run to the end of a cul-de-sac and returned. After 100 trials the door was removed and five of the nine animals shifted immediately to the shorter path without going into the blind alley. Higginson believes that this means that vision may play a rôle in the orientation of the animals. Valentine (161), however, has repeated this work (using a different maze) and found that of 19 rats only 4 made the sudden adjustment to the open door on the first trial after the training series, and on the second trial only 2 went through the door while 17 ran past as was usual when the door was not opened until their return. Higginson in his discussion implies that visual cues were the only cues changed and that the rat which made the sudden adjustment did so on a visual basis. Valentine implies that in his experiments other cues than the visual may have been changed. However, neither gives any data indicating what cues, if any, other than visual, were really functioning in these experiments.

Weaver and Stone (175) find no effects of blinding animals upon maze learning. Walton (164) uses a maze in which all cues, save vision, are manipulated so that they cannot be used in orientation and finds that the animal can learn. While this apparatus is called a maze by the experimenter it seems to be essentially a multiple discrimination box. Yoshioka (181) mentions an observation which would seem to indicate that the rat notices his visual environment.

2. *Olfaction.* Liggett and Liggett (89) find that anosmic as well as normal rats learn the brightness discrimination habit. Lindley (95) finds the same result for brightness discrimination but the anosmic rats were poorer on the maze. Rats which were both blind and anosmic were particularly poor in learning the maze.

3. *Proprioceptive senses.* Hunter (70) trained animals on various types of double alternation spatial mazes and then on the double alternation temporal maze. He again finds that the animals show little or no learning in the double alternation temporal maze situation. Hunter believes that this is because the same proprioceptive cues cannot at one time lead to one response and at another time to a different response; therefore, in the temporal maze since all other cues lack orientational value the problem is insoluble for the rat. It is a soluble problem only for those species in which the proprioceptive cues have a cumulative effect or in which there is a symbolic process functioning.

Hunter and Nagge (74) in a later experiment gave a number of animals a process of training in a series of four T-shaped boxes in the first two of which they had to turn left and in the last two right. Some of these animals were blinded and some of these were able to run the temporal maze. They could not, however, extend the series beyond 1 l r r. Does this mean that in the rat there is cumulative effect of proprioceptive cues or that the rat is capable of using a symbolic process or both? The authors do not commit themselves on this question. However, it is the reviewer's opinion in view of the recent work on delayed reaction, that we are almost forced to the conclusion that the rat has an ability which is the same as, or at least analogous to, the ability of the human being to use symbols.

Dennis (24), as a result of studying the behavior of rats with various degrees of sensory deprivation, comes to the conclusion that proprioceptive cues alone are not sufficient for perfect maze performance. Dennis (26) in another experiment with an apparatus in which he claims that all cues, except those of a proprioceptive nature are ineffective, concludes that proprioception is not accurate enough to

explain maze orientation. Gengerelli (46) also questions whether kinaesthesia is sufficient to explain learning in the maze.

Macfarlane (98) taught rats a maze in the usual fashion. Then he filled it with water in such a way that, instead of running, the animals had to swim. He found that this change caused very little disturbance in error score. The same procedure except in the reverse order was also used with the same result. He maintains that the change from running to swimming, or *vice versa*, must have been a change in the kinaesthetic pattern and that, therefore, if kinaesthesia was effective in guiding the animal there should have been a disturbance.

Lashley and Ball (79) attempted to eliminate by double hemisections of the cord in the cervical region most of the proprioceptive impulses in rats which had learned a maze. They then retested these animals in the maze and found almost perfect retention. They believe that they eliminated or controlled all exteroceptive cues. They conclude that the best explanation of their results is that the maze habit is controlled by some sort of a central mechanism which will function independently of sensory cues.

It would be interesting to know if rats under the conditions of the Lashley and Ball experiment could learn the maze. For, even if we grant that the maze habit, after it is learned, is controlled by a central mechanism, still it seems logically necessary that this engram must be established originally through some sensory pathway or pathways.

4. *Miscellaneous experiments related to the question of sensory control.* Gengerelli (45), Higginson (61), Warden and Fox (172), Leuba and Fain (88), Patrick and Anderson (123), and Hunter (71) have studied among other factors the effect of rotation of the maze. Gengerelli and Higginson find no disturbance. The other experimenters, under certain conditions, at least, do find disturbance. It would seem that this problem should be completely and systematically reworked with the experience of these and previous investigators as a basis from which to start. Particular pains should be taken to find, in the cases where disturbance is evident, just what is the basis of that disturbance. Maze pattern is probably one of the influential factors in this experiment as in many others.

Dashiell (22) has performed a number of experiments which indicate that the animals show a "direction-orienting tendency." The animals in some way acquire a knowledge of the general direction of the food with reference to the starting point so that if physical obstacles are removed it will go to the food over a path which it has

never taken before. He concludes that this phenomenon must have an intraorganic basis. Gengerelli's (47) data, likewise, would seem to support this view.

Yoshioka (185) also believes that the rat learns the goal-direction as part of the problem. On the other hand Dembo's (23) experiment would indicate that the animal does not learn the goal-direction.

Other experimenters, as for example Borovski (3) and Hunter (70) have observed that blind alleys going in directions of food are entered more frequently than others. This may be the result of the "direction-orienting tendency" although it has also been described as the retroactive influence of the food and as an anticipatory error.

Hunter (71) and Patrick and Anderson (123) have studied the effect of the variation of a number of factors in the maze situation. Hunter got disturbance in his animals as did, likewise, Patrick and Anderson in the group of their animals which learned under constant conditions but which were tested later under changed conditions.

Still another experiment which may be included under the heading of cues used in learning is that done by Tsai (158). He found that 96 per cent of the entrances into blind alleys by 36 rats were made where turns inside and outside of blind alleys were in the same direction.

A summary of the above work would indicate that the following possibilities must be considered in further work on this problem:

1. That there is a certain sensory field or combination of sensory fields which the rat must necessarily use in learning the maze.
2. That cues from all sensory fields may be of approximately equal value to the animal and when he is deprived of one he can use the remainder in a fully satisfactory manner.
3. That some sensory cues are necessary but that they are relatively unimportant, as compared with other factors, in the total learning process, with the consequence that our crude indications of learning are not affected by changes in these cues.
4. That the cues which are used in one stage of the learning are not the cues used in the other portions.
5. That sensory cues are used only in the first few trials until the beginning of the formation of an engram and that from then on sensory cues are not necessary in order to correct this engram so that it will eventually guide the animal without error.
6. That the changes in stimulating conditions may upset temporarily the habit but this does not necessarily mean that from these conditions the animal is receiving orientational cues.

IV. FACTORS RELATED TO SPEED OR EFFICIENCY OF LEARNING

1. *Tuitional controls.* Tsai (157) has investigated the influences of guidance upon maze learning. He either withdrew this guidance abruptly or gradually. These methods differed in their results but in every case the animals which had had guidance made more errors than the standard group which did not have guidance.

2. *Sex.* Corey (18) finds a difference in favor of the females for all criteria in learning an elevated maze. He says that the differences are statistically significant although he does not give the usual measures which are used to indicate significance. Tryon (152) on the other hand finds that there is a sex difference in favor of the males. He suggests, however, that this may be owing to the fact that he always ran his female group after the male group in the same maze. This may have caused olfactory disturbances in the females.

3. *Drugs.* Hansen and Cooper (55) tested the thirteenth generation of a line of animals the ancestors of which, for the first ten generations, had been subjected to alcohol fumes daily, except Sunday, until a state of complete narcotization was reached. They used a simple multiple-choice box and the Watson circular maze as tests of learning. The results of each problem are given in detailed form for the alcohol animals as compared with the thirteenth generation of a strain in which no alcohol had ever been used. The two strains were originally derived from the same stock. The net result of their work is to show that alcohol, under the conditions of administration in this experiment, has little, if any, effect upon learning.

The reviewer may add that upon two separate occasions, experiments concerning the effect of feeding alcohol upon learning have been done in his laboratory without any observable effects so far as total learning scores were concerned.

Macht and Leach (101) report an experiment on alcohol but the reviewer has not had access to it.

Miles (116) gives a short report on the effects of various drugs but no detailed data are published. He makes the statement, however, that no drug has yet been found which will improve responses in the maze as compared with the normal.

4. *Preferential tendencies.* Yoshioka (179, 186, 188) and Gengerelli (49) find that rats will group themselves roughly into those which tend to go right and those which tend to go left. Yoshioka believes that the curvature of the median suture of the nasal bones is related to this tendency. Peterson (124) also finds that some animals are right-handed, some left, and some ambidextrous. If

these observations are correct, then it is quite likely that these tendencies will influence, to some extent, the efficiency of the various animals in learning a maze.

MacGillivray and Stone (99) believe that a tendency to alternate is responsible for some of the errors made in learning the multiple light discrimination problem.

Dashiell and Bayroff (21) believe, on the basis of experiments in various mazes, that the rat has a forward-going tendency which operates in maze learning.

5. *Emotional disturbances.* Higginson (62) induced "fear" in some animals and "anger" in others before putting them in the maze. He finds these "emotional" disturbances to be detrimental to learning.

6. *Glands.* Tsai (156) finds that totally castrated, semi-castrated, and normal animals were efficient in learning, in the order given to both a problem box and a maze with the least efficient first.

Tuttle and Dykshorn (159, 160) report that castration does not influence maze learning if the castration and the learning take place before puberty.

7. *Length of maze.* Warden and Hamilton (170) study the relationship between length of maze and difficulty of learning in the linear pattern of the Warner-Warden unit maze. They find that the difficulty per unit varies inversely as the length of the maze and state that "this is quite opposite to the relationship obtaining in the memorization of serial language material." In the reviewer's opinion, this comparison is not fair because, in the unit maze used, the pattern is simply an alternation of right and left turns. These turns are not even 90 degree turns. Once the rat has learned to make alternate turns to the right and left then it is of little consequence how long the maze is. All that he has to do is to continue the application of the pattern until he reaches the food box. The situation is quite different in learning nonsense syllables. In this case, the human being can learn no pattern which is constant throughout the list.

Dennis (25) also gives some data on the problem of length and difficulty. His maze consisted of one true path and one blind alley. He simply increased the over-all length of this apparatus to see if it would cause any effect upon learning scores. He found none. A maze of this nature is probably too simple for the investigation of a factor of this sort.

8. *Age.* Liu (97), by the group average method, finds that ability to learn a maze increases from 30 to 75 days of age and that it declines from then on until the age of 250 days.

Stone (139, 140) has done a long series of experiments on the relations of age to learning. On the basis of these experiments he states, "For practical purposes it now seems sufficiently exact to say that in the absence of interfering habits, approximately maximum learning rate for mazes, problem boxes, simple light discrimination, and other novel situations thought to be of similar or equivalent nature is attained by young albino rats of 30 to 75 days. The majority of my experiments suggest that it is attained at an age nearer 30 than 75 days. The level of maximum learning rate in all probability does not decline in normal animals having no interference habits throughout the first two-thirds or more of their life span, i.e., during the first two years of life. Should subsequent experiments reveal a slight superiority for either the young, the adult or the early senescent group, there will, nevertheless, be found a very great amount of overlapping ability between the respective groups."

Tryon (152) by the correlation of age with scores in mazes finds a negligible relationship.

9. *Pigmentation.* Tryon (152) finds pigmented rats slightly poorer in maze learning than albinos. He suggests that this may be caused by the better vision of pigmented animals causing them to be more distracted by visual stimuli.

10. *Weight.* Tryon (152) finds that differences in weight are not related to maze ability.

11. *Vitamin deficiency.* Maurer and Tsai (106, 107) show that normal rats are about twice as efficient in learning as are rats with vitamin B deficiency.

12. *Ligation of arteries.* Chang and Liu (13) report that the ligation of one of the common carotid arteries impairs maze running to some extent and the ligation of the second one shows a still greater effect in most animals.

13. *Activity and learning.* Tuttle and Dykshorn (159, 160) find correlations ranging around .60 within litters between spontaneous activity and maze learning. The more active animals learn more readily. Corey (19) reports that compulsory physical activity has little if any effect upon the rat's ability to learn an eight cul-de-sac elevated maze.

14. *Distribution of practice.* Cook (15) and Mayer and Stone (108) find that in young animals there is no relationship between the distribution of practice and learning.

Mayer and Stone, however, report that one trial per day is better than three or five trials for adult rats. They are unable to explain the difference in results between the young and adult animals.

15. *Transfer.* Ho (63) used the mazes of Webb and Wiltbank and found some transfer from the one maze to the other. Hamill (51) finds, by changing animals from one maze to another, that the sequence of turns is of more importance in maze learning than the distance between turns.

16. *Whole versus part.* Hanawalt (53) has reported Pechstein's experiment using, however, a different maze. The author finds the whole method to be better than any of the part methods.

17. *Genetic factors in relation to learning.* Burlingame and Stone (8) report a correlation of .31 for litter mates on a multiple-T maze. Corey (17) finds correlations much higher than this for litter mates which learned an elevated maze. Tryon (150) reports the beginning of a research in which he is trying to develop two strains of animals, one good learners, the other poor learners. His strains have separated at the F2 generation although they are not, of course, genetically pure at that point. Tryon believes that, from the hereditary standpoint, "differences in ability to learn are probably multiple-factorially determined."

Other papers by Tryon (151, 152, 153, 154, 155) which bear more or less directly upon the question of the genetic basis of learning ability have been mentioned elsewhere in this review.

McDougall's (110, 111) experiments with reference to the Lamarckian hypothesis also have a bearing on the question of the genetics of learning ability. McDougall finds that succeeding generations of rats learn a problem with progressively greater ease. He believes that he has controlled all factors in such a way that the Lamarckian hypothesis remains as the only satisfactory explanation.

Hazlitt (56) has adversely criticized, on several scores, McDougall's experiment. This criticism was based upon McDougall's first report (110).

It should be pointed out that McDougall's experiment has a virtue which is not found in many of the experiments on the inheritance of acquired characteristics. This virtue lies in the fact that the characteristic which he is testing is a biologically useful one, namely, escaping from water, whereas in many such experiments the characteristic is detrimental to the animal. This fact may account for his results as compared with most experiments on this problem.

18. *Type of maze.* Miles (117) ran animals one trial per day in each of two types of maze, viz., the elevated type and the conventional type. The pattern was the same in the two. He finds that it takes a few more trials but less errors and time to learn the elevated as compared with the conventional type of maze. He suggests that the

superiority of the elevated maze may be due to its smaller surface area to be explored.

19. *Motivation.* The work on motivation done at Columbia with the obstruction method will not be reviewed here because the method does not involve, presumably, habit formation. The reader is referred to the section on book reviews for a review of this work by McAllister.

Warden and Haas (165), Hamilton (52), and Roberts (125) have investigated the question of the effect of delayed feeding upon speed of learning. The results in general indicate that delayed feeding slows the learning process. All experiments, however, are not in agreement concerning the relationship between the length of delay and the amount of retardation. Hamilton finds that there is no increase in retardation in learning a maze for delays of three, five, and seven minutes over one minute. Roberts finds that there is a progressive increase in retardation with delay periods of five, ten, and thirty seconds. His work was done on a problem box. Warden and Haas find no effect of five minutes' delay as compared with immediate feeding but a one minute delay causes a retardation.

Warden and Diamond (171) find that the effectiveness of punishment decreases with an increase in the interval separating the act and the punishment.

Valentine (163) reports that the effect of introducing punishment for entering blind alleys in a maze varies with the stage of learning at the initiation of the punishment. However, in all cases, punishment (electric shock) causes a decrease in the total number of errors made during learning as compared with the condition of no punishment.

The question of what is the most effective incentive to use in learning experiments has been again attacked by several investigators. Stone and Sturman-Huble (136) find that, for one-year-old male rats, food and sex are of approximately equal value for maze learning. Warden and Aylesworth (166) report that food and punishment are best as compared with either food or punishment alone in learning the brightness discrimination problem. This is especially true when the criterion of learning is a rigid one (18 errorless runs out of 20 trials or 27 correct out of 30).

Two experiments deal with the relative value of food as compared with escape-from-water. One of these by Ruch (130) shows that food is the more effective incentive for maze learning. The other by MacGillivray and Stone (100) finds no difference in the effectiveness of food alone as compared with food plus escape-from-water.

Ligon (94) has done an extensive investigation on the value of a number of different incentives and combinations of incentives. He used a peculiar maze in which only time scores could be taken. The number of different comparisons he makes is too great to permit enumeration here. It is sufficient to say that he found food combined with the sound of a buzzer in food box to be the most effective incentive of all those used.

Sharp (132) finds that more or less continuous running of a maze after it has been learned has a disintegrative effect on performance whether the animals receive reward or whether they do not. However, this effect is greater in the animals which did not receive reward.

A considerable number of experiments on motives and incentives have come from Tolman's laboratory. For a discussion of the theoretical implications of these and many other experiments the reader is referred to Tolman's recent book (148). Briefer discussions will be found in the articles by Tolman (147) and by Elliott (33).

Elliott (30) changed the reward from bran mash to sunflower seed before the maze was entirely learned. He reports that the error and time scores increased.

Blodgett (2) ran groups of animals in a maze for a number of days without giving them food in the food box. He then started giving them food and found that their learning curves dropped very rapidly. From this he concludes that "Non-reward running definitely develops a *latent learning*, and such latent learning is made manifest when reward is introduced." The question arises in the reviewer's mind whether it is correct to speak of the group which did not receive food as a "non-reward" group. Isn't it possible that removal from the maze acts as a reward?

Elliott (31) studied the combination of incentives and motives upon maze learning, and also the shift from one incentive to another which did not correspond so closely to the drive in the animal. Elliott (32) continued this work by running an experimental group of animals which were thirsty when put in the maze for the first nine days, and they received water as an incentive. On the tenth day and thereafter these animals were hungry (but not thirsty) when put in the maze and they received food as an incentive. On the tenth day these animals made a poor record as compared with the control group. On succeeding days, however, their records were comparable to the controls. Elliott says that this phenomenon "may be attributed to 'expectation' of a reward unsuited to the new drive (*i.e.*, hunger)" on the tenth day. Is it necessary to give an explanation in terms of

"expectation"? We have already seen (see above) that a change in stimulating conditions in the maze complex will temporarily disturb the animals. The shift from a physiological state of thirst to one of hunger is such a change and, therefore, it is not unusual that there should be a temporary disturbance in the animals.

Williams (176) taught animals a visual black-white discrimination habit. The white box (positive stimulus) was then used with these rats as an incentive at the end of a maze. There was no food in the box, however. She finds that this white box which had been associated with food in the discrimination situation acts as a reward to the animals when placed at the end of the maze. Its reward value, however, decreased unless the food was occasionally given with the white box.

Tolman, Honzik, and Robinson (144) report that the degree of hunger in the rat when put in a maze is one factor determining the order of elimination of long and short blind alleys. The hungrier the animal the less frequently does he attempt to enter the long blinds of the maze.

Bruce (7) ran an experimental group of animals for ten days with food as the reward. On the eleventh day and thereafter these animals did not receive food at the exit of the maze. He found that the performance of these animals was seriously affected by lack of food as a reward.

Tolman and Honzik (146) ran four groups of animals: (1) hungry non-rewarded, (2) less hungry rewarded. (3) less hungry non-rewarded, (4) hungry rewarded. The reward was food. The fourth group made the best record. The third group made the poorest.

Tolman and Honzik (145) performed another experiment in which they used two groups of animals, one group ran the maze with reward, until the eleventh day when it was removed; the other ran without reward for the same period of time at the end of which reward was introduced. The rewarded group deteriorated in their performance upon the removal of reward, while the introduction of reward to the non-rewarded group was followed by a sudden large drop in errors. This result is a substantiation of Blodgett's (2) work on latent learning. In fact Tolman and Honzik suggest "that latent learning may be more effective than overt learning."

20. *Surgical interference with the nervous system.* A discussion and review of material bearing upon this topic will be found in an article by Hines (59).

Lashley is, of course, the chief contributor of articles on the effect

of surgical interference upon learning. However, articles by other experimenters will be reviewed first.

Cameron (12) finds that lesions in the cortex have a detrimental effect upon both learning and retention. This controverts some of Lashley's earlier results. The explanation of the difference probably lies chiefly in the greater difficulty of Cameron's mazes as compared with Lashley's.

Buytendijk (10) also finds that cerebral lesions change the performance of the animal in a maze as compared with the normal rat.

Freeman and Papez (39) report results which tend to show that there is a positive correlation between the amount of subcortical injury (in superior colliculi and sensory thalamus) and retardation in the learning of a visual discrimination habit.

Loucks (96) studied the effect of cerebral lesions upon delayed reaction as measured by delay between trials in an apparatus similar to the Hunter temporal maze. The delay period used was fifteen seconds. He finds that marked interference results from cerebral lesions in the frontal lobes. This is true whether animals were trained prior to or subsequent to the production of the lesion.

Lashley (78) presents a large amount of experimental data and also theoretical implication in a book which it is impossible to review here. The experimental data are derived both from maze and brightness discrimination problems.

With reference to maze problems, Lashley and Ball (79) have published an article in which they show that the rat can still run a maze which it has already learned even when its spinal cord is cut in such a way as to eliminate presumably the great majority of proprioceptive impulses from the higher centers. This work has been mentioned above in connection with the discussion of sensory cues in learning.

Lashley (82) has also investigated the influence of cerebral lesions upon the threshold of brightness discrimination. He finds that the differential threshold for brightness is impaired by lesions in the visual cortex.

In still another article (86) he states, among others, the two following conclusions:

"1. Interruption of the optic radiations at their point of emergence from the internal capsule abolishes all capacity to react to visual objects, although the ability to distinguish between light and darkness is retained.

"2. Destruction of a small area in the lateral part of the area striata of the cortex abolishes the capacity to distinguish between

visual patterns, but leaves the capacity to distinguish the position and to some extent the distance of visual objects. Two objects differing in size may be distinguished, but only on the basis of their total luminosity."

The technique used in this experiment for testing pattern vision, etc., was the "jumping technique" which was mentioned above.

Lashley (87) in a lecture delivered before the Harvey Society summarized some of his work and gave his theoretical interpretations of his results. Also in his presidential address before the American Psychological Association (84) he discussed the relation of the nervous system to behavior. This discussion is based partly upon his own work and also upon many other lines of evidence.

Lashley's interpretations of his results have been challenged by Hunter (72, 73). The argument seems to be based chiefly upon Lashley's concept of equipotentiality of the cortex. Hunter argues that Lashley should not say that the cortex has equipotentiality in the absence of exact knowledge concerning the sensory control of the maze (see sensory cues above) inasmuch as his theory is based primarily upon the results obtained with that problem. He argues that the maze habit both in the learning and in the perfected habit is probably under the control of a multiplicity of sensory cues. Therefore, the removal of any particular portion of the cortex would not entirely destroy the habit inasmuch as the animal could still use the remaining portions and the sense organs connected to them. However, the more the cortex removed the greater would be the impairment, since this is equivalent to the removal of sensory cues.

To the reviewer, this is one way of explaining equipotentiality, *i.e.*, the equipotentiality of sensory cues in the maze habit is the basis of the equipotentiality of the cortex inasmuch as the different sense organs have different sensory projection areas in the cortex. However, Lashley (85) in his reply to Hunter says "the projection areas have, in addition to their specific sensory or motor functions, a non-specific (perhaps facilitative) function in which they are equipotential." It is evident, therefore, that to Lashley the equipotentiality of the cortex is not based upon the equipotentiality of sensory cues. In support of this view he cites his experiment on blind rats which learned the maze and which then suffered an impairment of the habit as the result of an occipital lesion. This evidence approaches the crucial in support of his position if it can be shown definitely that injury to the occipital area did not interfere with any pathways to other sensory projection areas.

However, Lashley is not inclined to admit that the maze habit

involved a multiplicity of sensory cues, at least, after it is perfected (see Lashley and Ball, 79). On the basis of his data he leans toward the view that the perfected maze habit is entirely under central control. While this is not the orthodox behavioristic view there are many lines of evidence converging toward the position that the peripheral mechanisms are of minor importance so far as orientational tendencies are concerned. These lines of evidence are derived from work on both human beings and the lower animals. We cannot enter into a complete discussion here but will mention only a few points.

Hunter speaks of a symbolic process in connection with some of the results upon the temporal maze. However, he says (72) that "a symbolic process may be peripheral as in the case of human languages . . ." He also speaks of a "neural engram" which he admits would be in the central nervous system.

Loucks (96) reports results of an experiment in connection with delayed reaction which would seem to be almost conclusive evidence against the possibility that slight muscular contractions are necessary for the maintenance of an orientational tendency. He gave rats a general anaesthesia during the period of delay in a delayed reaction experiment. The narcosis was sufficiently deep to cause the animals to fall over and remain quiet but, nevertheless, when they revived they could make the correct responses. This would seem to indicate that the orientational mechanism must be in the central nervous system.

These experiments of Lashley and Ball, Hunter, and Loucks would indicate, along with many others, that perhaps behaviorists have been overemphasizing the importance of the peripheral mechanisms.

It remains to be mentioned that Bartley and Perkins (1) have criticized Hunter for his criticism of Lashley, and that Melton (114) has also presented a criticism of some of Lashley's work.

21. *Retention of habits.* For a general review of the literature on retention in animals the reader is referred to the article by Schneck and Warden (131).

Corey (20), Heron (58), McNemar and Stone (113), and Tryon (154) have studied the retention of animals but the primary emphasis has been upon the magnitude of the correlation between learning and relearning and the factors which may affect this correlation. These results have been mentioned above in connection with reliability.

Apparently, no one has as yet made a thoroughly systematic study of the curve of forgetting for the rat.

V. HIGHER MENTAL PROCESSES

1. *Delayed reaction.* Honzik (64), Loucks (96), and Maier (103) have all investigated delayed reaction in the rat. None used the same method and none used the method originally used by Hunter. Honzik's procedure most nearly approached Hunter's, the chief difference was that the animal was allowed to make a response to the stimulus before he was delayed. Under these conditions a delay of forty-five seconds was obtained without gross orientation. Loucks adapted the temporal maze to the delayed reaction procedure and secured delays of five minutes and the rats were still apparently short of their maximum. This method, however, allows the use of only two possibilities. Maier used three pathways to food. He ran the rats on one of these pathways three times in succession and then removed the animal from the room. After the period of delay which in some cases was several hours he returned the animal to see if it would take the pathway which it had previously traversed.

All of these experiments, therefore, show much longer delays for the rat than had previously been reported. This gives further emphasis to the view that the results of an experiment are almost as much a function of the technique as of the organism.

Clements (14) has performed an interesting experiment which is somewhat allied to the delayed reaction problem. He constructed an apparatus with two paths to the goal, one of them ten times as long as the other. The rat was allowed to take his choice of the two paths but could be delayed at the will of the experimenter immediately after making the choice. He found that a 120 seconds delay was long enough to prevent the animals from learning to take the shorter of the paths.

2. *Abstraction.* Gengerelli (48) finds that the rats are able, in a limited way, to learn identical elements in a situation although there is a variation in the concomitant elements. This would indicate that the rat has the ability to form concepts.

3. *Reasoning.* Maier (102) did a long series of experiments on a few animals "to learn whether or not rats can solve problems without 'trial and error'." On the basis of his results he concludes that rats can reason. Maier (105) in another article writes a theoretical discussion of reasoning and learning in both animals and human beings.

4. *Attention.* Maier (104), by introducing into a maze situation

a stimulus to which rats had previously learned to react positively for food, believes that he has demonstrated that part of the errors in a maze are caused by the inattention of the animal.

5. *Tools.* Fritz (42) reports an observation on rats in which the animals were seen to use wood shavings as a means of securing water. He believes that this indicates that these animals are capable of using tools.

VI. THEORY AND EXPERIMENTS DEALING WITH THE FUNDAMENTAL NATURE OF LEARNING

The experiments discussed here have been separated in a very arbitrary way from many of those already mentioned. The experiments dealing with cues used in learning and those on surgical interference could be very well placed under this heading. However, it seemed better to the reviewer to discuss them separately.

1. *Frequency, recency, and primacy.* The following experimenters have contributed experiments on one or more of these factors: Gengerelli (44), Higginson (60), Yoshioka (178, 186), and Warden and Cummings (168). It seems quite obvious from these experiments and many others in both the animal and human fields that frequency and recency, at least, are not of themselves causal factors in the learning process. It still remains a fact, of course, that in order for most problems to be learned the situation must be repeated frequently. However, the repetition is not what causes the learning or unlearning but, rather, because of the repetition of the situation other factors are allowed to operate which produce the desired effect.

2. *Experiments related to the Gestalt theory of learning.* Many experiments already mentioned bear upon the Gestalt theory. Among these, and others, are those done by Buytendijk (11), Gayton (43), Gilhousen (50), Helson (57), Hsiao (65), Maier (102), and McDougall (112). All of these experiments and many others tend to show that if anyone ever seriously believed that behavior can be explained by any simple S-R formula then that opinion must be modified or else maintained dogmatically in the face of experimental findings. On the other hand, the reviewer seriously doubts that we are helped to a fundamental understanding of behavior by the use in connection with it of such terms as "insight," "Gestalten," "structure-function," etc. Such terms are admissible from the standpoint of descriptive exposition but it is the reviewer's opinion that a real understanding of the behavior can only come through a thorough analysis of the mechanism of the organism in relation to the situation

in which the organism is placed. This is a task which will require the coördinated efforts of anatomists, neurologists, physiologists, biochemists, statisticians, and psychologists.

3. *Theoretical treatises.* Tolman (148) sets forth a system together with a great mass of experimental evidence. This is mentioned here because of its great importance, although it does not fall in the period under review.

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EFFECTS OF CASTRATION ON THE BEHAVIOR OF MAMMALS

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Previous reviews of the effects of castration on behavior in the higher animals (37, 44, 48, 64) have indicated that alterations in behavior are temporally correlated with physiological and somatic changes. As yet, however, causal relationships existing between these behavior phenomena on the one hand and the physiological and somatic changes on the other are little known. It is presumed that many changes result directly from the elimination of gonadal hormone from the blood stream, yet, by similar reasoning, it may be inferred that others are but secondary effects of altered somatic structures.

BASAL METABOLISM

The majority of observers have reported a lowering of the rate of basal metabolism after gonadectomy in mammals (1, 7, 10, 14, 31, 33, 34, 50, 54, 58, 70). Loewy and Richter performed the classical experiment in this field (38). They determined the oxygen consumption in a male and female dog before and after gonadectomy and found a reduction of over 15 per cent in the female and a slightly smaller amount in the male. A parallel study from more recent times offers an interesting sidelight on the disagreement among students of the subject as well as a possible commentary on technique and other factors involved. Bugbee and Simond (9) studied the effect of castration upon metabolism in a male dog and found a reduction of 44 per cent after the operation. They also found, however, that the basal metabolism of a non-operate normal female was reduced 35 per cent over the same period of time. They conclude: "We believe that under experimental conditions other factors play a greater rôle in the reduction of metabolism than does castration. Factors to be considered are lack of psychic stimulation, lack of muscular exercise, adaptation of the nervous system and endocrine gland system to a life calling for less metabolism than in an active normal life." Injection of the follicular hormone into women raises the basal metabolic rate (14).

Slonaker (61) reported that the food intake of castrated males was only about half that of normal animals, but as he also found a still greater difference in the activity of the two groups, this latter factor evidently should be taken into account. Dubois (16) apparently inclines to the view that the lowering of the metabolic rate after gonadectomy is not a consistent sequela of the operation. Korenchevsky (33) suggests that the results obtained in the experiments are "due not only to the direct influence of the gonads but also to secondary changes in the thyroid, hypophysis, adrenals, and pancreas, and to the efficiency of these glands before castration."

NERVOUS SYSTEM

Data relating to the effect of castration upon the nervous system should also be of interest to the psychologist. Donaldson and Hatai (15), working with rats, reported that castration reduced the weight of the brain and of the spinal cord only slightly and that there was no difference in the water content of the nervous system. Hatai (23) confirmed these negative results in a later study. Such differences as did appear were not confined to the cerebellum, as Gall had believed, but were proportionately distributed throughout the whole brain. Kadanoff (30) studied the effect of castration upon the nerve endings in the genital organs of mice. Although the animals were castrated shortly after birth, the nerves of the penis were found to continue their development, with complicated nerve endings and a rich supply to the tissues. Blotevogel (8), working with the female mouse, found that gonadectomy was followed by chromatolysis and a reduction in the number of chromophylic cells in the paracervical ganglion of the uterus. Melchior and Nothmann (46), in their experiments on rabbits, reported a change in the electrical excitability of the peripheral nervous system after partial or total loss of the testes. This seemed to be a form of over-excitability which, they concluded, was probably caused by a disturbance of the whole endocrine system.

REFLEX ACTION

Recently an attempt has been made to correlate the time of reflex action with functional changes in the gonad. Herren and Haterius (24) measured the Achilles tendon reflex as it was affected by the different stages in the oestrus cycle of the rat. They found that the time of reaction was shorter during dioestrus than at oestrus. Injection of estrogen into female castrates was also found to lengthen the reaction time while lipo-lutein shortened it. Their conclusion

was that the follicular hormone causes a heightened activity of the higher nervous centers, since it is their belief that "variability in reflex time is the result of functional disequilibrium in the inhibitory action of the higher and lower irradiational centers." The authors believe that the reported changes in behavior following changes in the sex cycle or after castration, implantation, etc., are essentially reflections of changes in tone of the different nerve levels, due to the influence of the sex hormone.

As a possible basis for understanding any changes in activity due to castration, the following studies would be of interest. Parhon and Kahane (52) reported that the muscles of castrated guinea pigs contained less calcium and more magnesium than those of the control animals. Parhon and co-workers (53) also found the water content of the same type of tissue to be diminished after a short period of increase. Jasienski (29), who made histological studies of muscular tissue, reported that, in some castrate animals, the muscle fibers were thinned and the connective tissue relatively increased. This might be correlated with the greater fatiguability of castrate muscle preparations. Gans and Hoskins (20) isolated the gastrocnemius muscles of castrate rats and studied the amount of work performed. They found that, although the weight of the muscles was greater in the castrate animal and the absolute strength of the fibers averaged about the same as that of the normal controls, nevertheless, the total work performed by the muscles from the gonadectomized animals was considerably less than in the case of non-castrated rats. They imply that this greater fatiguability may be due to the inadequacy of supporting functions such as circulation or respiration. Other studies (22, 47) have confirmed these experimental findings. Athanasiu and Pézard (4) reported that castration reduced the motor energy of cocks from 20 to 30 per cent, as measured by the action currents of the gastrocnemius muscle during voluntary walking.

Offsetting the foregoing claims, to a certain degree, are the well known facts concerning strength and endurance of castrated cattle employed as draught animals and the speed and endurance of geldings whose training and occupational history are similar to those of normal animals. There is no manifest inability of geldings to live up to their precastration potentialities for speed and endurance on the race track.

VOLUNTARY ACTIVITY

Many successful experimental attempts have been made at linking changes in the spontaneous activity of female rats with rhythmic

changes in, and with the presence and absence of, the ovary (60, 73). Hoskins (25, 26, 28), Slonaker (61), Wang (73), and others have shown that a similar reduction in spontaneous activity takes place in the male after castration, although the amount of change is not so great as in the female after ovariectomy. Testis grafts (26), injection of testicular extracts (28), or testis feeding (18), however, apparently had no significant effect in raising the level of activity of the castrate. Ovarian feeding (17) also had no effect on the voluntary activity of castrate female rats. Gans (18) found no difference in the loss of activity in rats castrated after puberty when compared with those castrated prepuberally. Both suffered the same amount of decrement. The same author (19) reported in a study on fractional castration that the fall in activity after removal of one testis was only slight while the most marked changes were observed after removal of the last fraction of the second testis.

Richter, Wang, and co-workers (57, 74) have investigated the effect of both ovarian and testicular transplants on the spontaneous activity of gonadectomized male and female rats. They found an increase in activity that was correlated with the state of preservation of the graft. The increase in activity brought about by the transplanted testis, however, was much less than that due to the engrafted ovary. Hoskins (27) suggested that the depression of activity after castration in rats is due to the accumulation of fat. He found that when his castrated rats were subjected to four or five days of starvation, the spontaneous activity increased about 200 per cent. After full feeding, the activity level was again slowly depressed. Combermale (11) observed a reduction in the vivacity, playfulness, and general activity in two male dogs castrated in infancy. These dogs were compared with two intact littermates which were reared in the same household and similarly treated.

Removal of the anterior pituitary gland in male and female rats produces approximately the same reduction of voluntary activity as does ablation of the gonads, according to Richter and Wislocki (57). It is believed by them that the anterior hypophysis elaborates a hormone which activates the gonad. This belief has been substantiated on other grounds (Smith, 62).

SEX BEHAVIOR

a. *In the Male*

The influence of castration upon sex behavior of the male has of course long been known. Stone (64) has summarized some of the experimental studies that would throw this relationship into clearer

light. He reports that "practically all observers agree that castration of vertebrates in early infancy results in total or almost complete suppression of all sexual responses. Castration after early infancy and up to or including the age of puberty causes changes in activity which are determined in large measure by the physiological age of the animal, but which vary considerably according to the species." Nothing in the recent literature requires a revision of this statement.

The retention of copulatory ability by male rats castrated at the age of 90 days has been observed by Stone (66) in some animals many weeks after castration. Of the 42 males tested, approximately one-third ceased to copulate during the first month after castration; by the end of the second month, 45 per cent had dropped out; 57 per cent by the end of the third; 74 per cent by the end of the fourth; 79 per cent at the end of the fifth; and 90 per cent at the end of the sixth month. No cases were active after the eighth month. A similar study of 23 male rabbits (67) yielded data in essential agreement with those for the rat, although the duration of aggressive sexual behavior was less, it being approximately one month for a young adult animal. In a few extreme individuals copulation with intromission occurred as late as two months after castration; and mounting with pelvic movements were executed for an additional five months period. Stone found (66) that "exercise of the copulatory function alone would not insure the persistence of sexual aggressiveness and the copulatory act" nor would it "prevent the onset of the usual post-castration atrophy." Other factors, accordingly, must be involved in the production of sexual behavior beside the mere presence or absence of the gonads. What they are, however, cannot be stated at the present time. The same author in an earlier study (63) on the contribution of certain sensory functions to sex activity was able to rule out a good many possibilities. "The initial copulatory response can be aroused in sexually inexperienced male rats when afferent impulses from all of the following sources have been excluded: the skin of the anterior belly wall, the inguinal region, and the ventral and lateral portion of the scrotum; from the vibrissae; and from the visual, olfactory and gustatory receptors, and auditory receptors in a diminished degree." Other investigators have also removed the prostate and seminal vesicles from animals with apparently no effect on sex behavior (44, 61).

It is fairly certain that sexual desire in the human male is reduced in strength when the gonads are removed at any time prior to puberty. Following postpubertal castration (limits not yet deter-

mined) copulatory ability and the sexual desires are said in isolated cases to be unchanged for a short period of time. In most cases, however, loss of sexual desire or impotency gradually follow. The efficacy of total castration for reduction of sexual libido in subnormal individuals, criminals committed for sexual offenses, and others whose abnormally strong lust makes them a menace to society is emphasized by Barr (6). He states that no bad effects resulted from the castration of 18 individuals who because of inordinate sexual passions were intractable, and that, in view of the quieting effects on the sexual passions, the results were on the whole satisfactory. Essentially similar results were reported by de Quervain (55). His materials consisted of 32 cases, 27 of which were males and 26 of which had been in conflict with the law. Investigations subsequent to castration showed that the libido was more or less reduced in almost all of the cases. Castration rendered 14 impotent; in 12 potency was reduced; and in a single case no change was apparent. Generally speaking, the effects of castration were experienced within a month, though in some cases libido remained unaltered, so far as the subject could discern, for two or more years. De Quervain states that the final effect was generally correlated with the intensity of the libido before castration.

Certain heterosexual and homosexual practices are known to take place in the case of eunuchs. Frequent copulations twenty years after the operation was reported in one of the case studies of Tandler and Gross (68). McCartney (39) examined 23 Chinese eunuchs and 3 *Spopecs*. Some of the subjects had been deprived of the external genitals. Ten of their number had gonorrhea and one an active chancre at the time of their examination. Most of the individuals still in possession of the penis testified that they had frequently indulged in sexual intercourse with prostitutes. They also claimed to have indulged in homosexual practices and other perversions as well.

A case described by Rowe and Lawrence (58) is particularly instructive by way of showing how the mental habitus may be altered after castration and restored by psychological factors. They described a robust young man who was completely castrated at the age of twenty-five years. Subsequently he developed a profound depression and was forced to give up a varied and interesting career. Nine years later this individual, who meanwhile had settled down in a quiet community and by virtue of varied experience and general culture derived from domestic and foreign travel had become a highly esteemed member of the younger group, married a young woman who

was fully acquainted with his condition. Statements given out later relative to his sexual life indicated that the man was capable of rendering an account of himself entirely satisfactory to both parties. In his case more or less complete mental, social, and economic rehabilitation was achieved without recourse to any type of gonadal therapy.

b. *In the Female*

Mammalian females below the level of monkeys, and possibly including certain species of monkeys, cease to become receptive after a total removal of the ovaries. Hammond (21) found that rabbits in heat at the time of castration could be mated for about 48 hours, but never thereafter. This result is particularly striking in view of the fact that the female rabbit is very receptive, as a rule, and contrary to the rule for lower animals will permit copulation during the period of pregnancy (14, 32).

But few data of a well authenticated character are at hand concerning the alterations in sexual desires and sexual reflexes in women after total castration, yet the frequency with which testimony to the effect that little change is noticeable in those whose sexual inclinations were previously strong would seem to warrant much conservatism in ascribing to any form of gonadal therapy the return of sexual libido unless something simulating controlled experimental conditions are observed in the collection of the data. Mansfield (42) reported that of nine cases with normal sexual desires at the time total castration was performed, six retained the libido sexualis and four retained the reflexes and experienced the voluptuous sensations associated with the orgasm. Frank (14) says that numerous observations carefully controlled have fully convinced him that women, after double ovariectomy, undergo no diminution in their sexual desires. The same applies to those who have passed through the normal menopause. Of particular interest is a case cited by Frank in which postmarital reports were obtained from a young woman who at the age of twenty years had undergone double ovariectomy because of bilateral carcinoma of the ovaries. She was married the following year. After six years of married life she reports that sex desire is present, is well developed, and that intercourse culminates in the typical orgasm. The individual alleges that she had never had intercourse prior to marriage, nor had she experienced strong sexual inclinations toward men prior to her operation.

Evidence corroborating the statements by Frank have also been made by other observers (58, 72).

Restorative therapy as applied to copulatory behavior in animals has met with variable success and is difficult to evaluate owing to our lack of knowledge of the potency of therapeutic agents and suitable dosage for the animal being studied. Allen and Doisy (2) in their earliest publication on the follicular hormone emphasized the fact that the follicular extract reactivated the mating instinct of castrated rats. In a subsequent publication (3) they stated that copulation was noted in 7 of 11 castrates receiving follicular injections. Frank (14) and others have obtained similar results with rats and mice. Marrian and Parkes (43), who injected various amounts of oestrin into mice for the purpose of determining what amounts could be relied upon to produce particular phenomena of oestrus, found that as little as 100 mouse units (1 unit being the amount of oestrin necessary to produce a cornified cell in the vaginal smear) did not produce the typical uterine oestrus, but that it was brought about by injections of 400 units. In Table 1 is shown the results for copulation as obtained by injecting various amounts of oestrin. They

TABLE 1
AMOUNT OF OESTRIN (GIVEN OVER 36 HOURS) REQUIRED TO CAUSE COPULATION
After Marrian and Parkes (43)

Amounts of Oestrin (Units)	Number Injections	Number Mice	Number Copulating
25	4	10	0
25	19	10	2
50	4	10	0
50	19	9	2
100	4	10	2
100	19	10	4
200	4	10	4
200	19	9	5

conclude that approximately 200 mouse units are required to induce copulation in castrated females.

Nissen (51) has studied the sex drive in rats with the obstruction technique. While orchitic extracts were apparently without effect upon the depressed impulses of the castrate male, placental extract was found to restore the sex drive of ovariectomized females. The refinements in the preparation of testicular extracts that have recently been attained (Moore, 48) would make a repetition of this experiment very interesting.

Knude, D'Amour, Carlson, and Gustavson (34) evoked the mating instinct in both a normal and a castrated dog by injecting estrin. Exceedingly large doses were required in each case. By means of injections of folliculin B, an impure water soluble prepara-

tion of female sex hormone, Zondek (75) was able to induce menstruation twice in a woman who had been castrated two years previously. An extensive review of literature by Vruwink and Popenoe (72) indicates that sterilization of women by ligation and severing the Fallopian tubes has no effect on sexual desire. Hysterectomy likewise produces no alteration. Bilateral ovariectomy has more drastic effects, they find, particularly in the cases that are under twenty and over fifty or more years of age. In healthy middle-aged women of childbearing ages, no effects whatever, or only slight diminution in libido was reported. Speaking of Dickinson's data, they report that in about 75 per cent of the cases reduction or elimination of sexual desire followed double ovariectomy. Vruwink and Popenoe very properly call attention to the fact that statements of the preoperation libido are absolutely essential for the correct interpretation of postoperative effects. They find that 25 per 100 married women interrogated do not report that coitus is pleasurable. Of this number 10 individuals say that it is distasteful and 15 say that the experience is neutral. Since this finding is in accord with that of other workers, too much stress upon the desirability of checking post- with pre-operation reports cannot be laid.

SEX REVERSAL

There has been reported a rather large number of studies on the feminization of males and the masculinization of females by means of transplants and gonadal extracts (37, 59). The psychic changes that have been described as following such procedures have not always been well controlled experimentally. Stone (65) has called attention to this in a report on the finding of "feminine" behavior in normal male rats, and believes that a statistical study should be made of the incidence of such traits among adult male animals before we can properly evaluate their appearance in the "feminized" ones.

The names of Steinach, Lipschütz, Voronoff, and Stanley have become closely associated with the technique of rejuvenation in man and animals (37, 64) through testicular grafting and ligation or resection of the vas deferens. Experimental studies have not been wanting to serve as a basis of expectation for realizing some of the supposed benefits of this procedure, but in the human clinical field the list of symptoms for which it has sometimes been claimed to work ameliorations has become so extensive as to cast doubt on the scientific value of much of this type of work. Such important factors as the power of suggestion, improved living conditions, rest, care, etc., have not always been controlled. Moore (49) has recently expressed sharp

criticism of some of these claims, after having carried on an experiment on the effect of non-living testis grafts in the rat. He maintains that the body does not retain the testicular hormone for any length of time, since it is excreted through the kidneys, and he could detect none objectively in animals with subcutaneous testis grafts. The grafts furthermore failed to delay castration changes in the rat for even as short a period as two days, and the author believes that there is no "acceptable evidence that non-viable testis grafts exert any immediate or remote beneficial effect on the host." It might be mentioned, however, that Retter and Voronoff (56) report that portions of testicle from anthropoid apes will "take" in man if implanted in the tunica vaginalis, and will live in that location for a considerable period of time.

LEARNING

A few studies have appeared recently which have reported on the relationship existing between the functioning of the gonads and learning or integrated behavior. Ball (5) investigated the effect of the female sex cycle upon the learning ability of the rat. Sixteen rats in oestrus and sixteen control animals were run on a simple maze with one cul-de-sac. No significant difference was found between the two groups in their ability to adapt to this simple situation. The simplicity of the maze employed and the use of concentrated practice periods were probably not very well adapted for demonstrating any fine differences in learning ability that might have existed.

Related to this topic is the work of Macht and associates (40, 41), who believed that they were able to find a detrimental effect of prostatectomy upon the ability of rats to integrate muscular movements, as measured by the facility with which they were able to run from one side of a room to the other on a stretched rope. They reported that the group of animals which had the prostate removed, took a longer time to learn, with progression much slower and more difficult. This was not characteristic of the control laparotomy operates. Feeding of dried prostate and other glands seemed to increase the muscular efficiency of the prostatectomized rats. These reports, however, are suggestive rather than conclusive, as the number of animals employed was small.

Lashley (35), incidental to another discussion, has reported that "we have tested the general activity of castrates as measured in revolving cages, in problem solving and learning, and find them not different from normals."

Tuttle and Dykshorn (71), in a study on the relationship between

spontaneous activity and the ability to learn, with special reference to castration and ovariectomy on these processes, removed the gonads from fifteen rats, taken from five litters, and employed the remaining twenty as controls. After their spontaneous activity was determined by the revolving cage method, and their ability to learn a maze as measured by the number of trials and of errors, their records were compared on the basis of litters. "In the case of litters 1 and 2, castration had no effect on either the learning process or spontaneous activity. . . . In litter 4 the castrates had a distinct advantage over the normal animals in all parts of the experiment. In litters 3 and 5, just the reverse is true since the normals have the advantage." Although the authors do find that "activity and learning are closely allied," the "data indicate that castration has no effect upon either the learning or the activity of white rats under the age of puberty."

Tsai (69) has more recently reported an experiment in learning a maze and problem box, in which he employed male rats, 12 totally castrated, 8 with one testis removed, and 7 forming a control-operate group, from which the gonads were not removed. All animals had previously learned a different maze. Although the time records from the problem box did not give a clear-cut picture, he believed that the time and error records on the maze indicated that the totally castrated rats were poorer than the control and semi-castrates. The author reports that the maze experiment was repeated upon two further groups, one consisting of 8 castrated animals, and the other of 8 controls. The small number of animals employed in both this and the preceding experiment reported, with the resulting inability of applying statistical safeguards to control chance factors, as well as minor questions of technique, would hardly furnish a basis for critical evaluation of the results.

One of the present authors (Commins, 12) has just completed an extensive study of the effects of castration upon the learning performances of male rats. The animals employed were reared under uniform conditions in the laboratory of the Department of Psychology, Stanford University. Assignment to the experimental and control groups was made by splitting up the litters in a chance manner. The experimental groups, consisting of from 30 to 40 individuals each, were castrated at 20, 50, 90, 130, and 170 days of age respectively. Their learning ability was compared with that of two control groups, one of which was given a "control" operation without the removal of the gonads, and the other group, the normal control, was untreated surgically.

Four laboratory instruments were employed in measuring the

learning ability of the castrate and control groups: (1) the Stone Multiple-T floor maze; (2) the Stone light discrimination box; (3) an elevated maze of the U-type; (4) an elevated maze of the T-type. Food was made the incentive for mastery of the instruments; all animals were reduced 25 per cent in weight in order to strengthen and control motivation. The rats were introduced to the learning instruments at 180 days of age, which was constant for all the groups studied. Fifty days after they had completed the original learning experiments, which occupied a period of forty-one days, they were brought back to the same instruments for relearning tests.

In comparing the records of the animals obtained from the learning instruments, it was found that the mean scores, calculated on the basis of errors, time, and number of trials taken to satisfy criteria of learning, showed differences no greater than might well be accounted for on the basis of chance factors alone operating. The castrated groups were not significantly poorer than the control groups, nor was there found any consistency of trend in the means of the castrate groups with respect to age at castration. Differences in the relearning experiments were smaller than those found in the original learning series.

The weights of the castrate animals were found to be lower at both 165 and 256 days of age than those of the non-castrate rats. The differences were found to be significant by the use of the critical ratio technique. It was also observed that the earlier the age at which the animals had been castrated, the greater was this inferiority in weight.

From the experiment as a whole, it was concluded:

1. That castration at 20, 50, 90, 130, or 170 days of age is not deleterious to the learning ability of male albino rats as measured by such instruments as the Multiple-T maze, the light discrimination box, and two elevated mazes.

2. That castration influences the growth rate of albino rats, and that the amount of inferiority in weight depended upon the age at the time of castration.

It is assumed that the peculiarities of behavior ordinarily associated with the castrate condition in man and animals cannot be explained in terms of any deep-seated modification of their inherent ability to learn. They may perhaps be sometimes explained on the basis of factors, as yet unidentified, which underlie the emotional and affective life.

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RELATION OF THE MALE AVIAN GONAD TO
RESPONSES PERTINENT TO REPRODUCTIVE
PHENOMENA *

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Causal relations between the avian testis and behavior associated with the physiology of reproduction have been inferred principally from three factual sources: (1) seasonal variations in the size of the testes of some birds are correlated with the incidence and alterations of sexual behavior; (2) females exhibiting the somatic signs of sex-reversal have been found to possess seminiferous tubules in the modified ovarian tissues; and (3) gonadectomy and transplantation of testicular tissue are followed by predictable modifications of sexual behavior.

Very gradual has been the growth of present knowledge of dependent relations between testicular activity and reproductive responses. In order that this point may be appreciated to the fullest extent, the author has followed, in so far as possible, the chronology of principal contributions in this review. In the final pages will be given a brief résumé of the principal factual contributions which will tend to offset the inevitable scattering that results from adherence to a chronological method.

Aristotle (64) gave a scale showing the progressive increase in the size of the testis of the sparrow from winter until spring and commented upon the relation of this increase to the heightened breeding activity. Tannenburg (66) in 1799 noted that the gonads were largest at the time when coition occurred most frequently.

In 1849 Berthold (8) made an experimental approach to the problem of the relation of the gonads to somatic secondary sex characters and behavior by means of the techniques of gonadectomy and of grafting gonadal tissue in the fowl. He found that after removing the gonads, thus severing its normal nervous, vascular, and connective tissue relations, and then grafting testicular tissue subcu-

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taneously, the fowl still functioned so as to maintain the somatic sex characters and psychosexual behavior. This experiment, which was overlooked for a long time by workers in biology and related fields, showed that the testis exerted its influence by means of a humoral medium. Yarrell (71) in 1857 gave a review of the effects of the gonads on the sex characters of mammals and fowls and said, "the capon will take a clutch of chickens, attend them in their search for food, and brood them under his wings when they are tired" (p. 81).

Knowledge of sex-reversal in the female fowl is reflected in the folklore of many peoples. In fact the cessation of the feminine functions and the exhibition of a degree of masculinity is well expressed by proverbs, anecdotes and rhymes. Yarrell (70) as early as 1827 reported in scientific literature a case of sex-reversal in the female pheasant. In this paper modification of the ovaries was mentioned as a possible causative agent in this change of the bird's anatomy and behavior. Brandt (11) studied the histology of the gonads in several cock-feathered hens, which, by calling other hens to food, by crowing, and by mounting during copulation evidenced masculine behavior. Brandt found seminiferous tubules in the right ovaries in many of these birds.

Etzold (25) in 1891 studied the seasonal cycle of change in the size of the testis in *Fringilla domestica*. The organs were approximately sixteen times as large in summer as in winter. He noted during the observations that one pair of birds copulated thirty times during six minutes, whereas another pair over an equal period of time copulated eleven times (quoted from Disselhorst [22], p. 114). It is interesting to note that Etzold by using the frequency of copulations during a definite time period as a measure of sexual activity was approaching the *time-limited systematic observational technique* which has been employed recently by Carpenter (16).

The experiments of Berthold (8) were repeated in 1898 by Foges (28) who confirmed the conclusions of Berthold; however, he found it difficult to perform complete castration in his fowls. Shattock and Seligmann (63) stated that in some of their incompletely gonadectomized birds the secondary sex characters developed normally. In one partially castrated male a nodule of tissue similar in size to that of a "hemp seed" was found. This bird "took no notice of hens with which it was habitually kept." The main issue of their work, like that of Berthold and Foges, was to establish the transplantability of the testis and to suggest the humoral mediation of the testicular influence.

Bouin and Ancel (10) summarized their important work of 1903 as follows:

We hold the interstitial gland, then, to be an organ which probably elaborates nutritive substances for the use of the germinal epithelium and that on its internal secretion the "ardeur genital" and the sexual characters depend. (Trans., p. 516.)

In an article published in 1904 these authors stated again that the interstitial cells function to maintain the "genital instincts" and that incomplete development of these cells caused abnormality of the secondary sex characters and the sex instincts.

Pézard (51) in 1911 repeated the work of Bouin and Ancel on the fowl and showed definitely that the gonads were influential in determining normal secondary sex characters and characteristic sex instincts. Pézard and De Cilleuls (21), during the following year, worked with young cocks and arrived at the conclusion from this work that the ontological development of sex behavior paralleled the appearance and hyperplasia of the interstitial cells among the seminiferous tubules of the testis.

Goodale (32) in 1913 continued important work begun in 1910. He described briefly the normal behavior of the male fowl, saying that it had an erect carriage, was pugnacious, crowed frequently, but apparently lacked the brooding instinct. Seven cockerels were castrated when they were about twenty-one days old, and in those that lived until they were sixteen months of age, the sexual instincts were undeveloped. Goodale reported that in one bird which showed some signs of attending to hens an autotransplant was found at necropsy. In a more complete account of his work in 1916 (33) Goodale said, in discussing the behavior of a bird which had been castrated before puberty: "His behavior is anomolous, in that, although usually quiet and noiseless, he sometimes crows, sometimes shows the male sexual reactions and may brood chicks" (p. 51). The capon according to Goodale is not pugnacious and will seldom fight. It lacks aggressiveness and sex "desire," but will respond to a sex object if the specific visual stimulus is *reinforced*. The response of the capon as compared with a normal cock is reflex-like and not characterized by quickness of movement and aggressiveness. The animals that apparently behaved in a normal manner had varying amounts of gonadal tissue which remained *en situ* after the operation. Much confidence may be placed in the work of Goodale. However, one finds that he mentioned no procedure which would be adequate for the study of behavioral changes following castration. His general

observation that the sexual reaction is an interaction between two individuals, hence social in character, and depends on the psychological states of both participants, is both interesting and important.

After studying cocks castrated when young, Pézard (52) in 1918 reported that they were without normal evidence of the sexual instincts. When the operation was performed after maturity, degeneration of the comb and gills began immediately, and in a *few days* this change was followed by a loss of the sexual instincts. Pézard found that normal sexual characteristics may be restored in the capon by grafts of testicular tissue or by injections of a solution made from the testis of a pig. Furthermore, a very small fraction of the normal amount of testicular tissue was found to be sufficient to maintain normal sexual behavior. When an attribute of sexuality did appear it was developed fully or not at all. About 0.3 per cent of the testes of a normal fowl assure the development and maintenance of the secondary sex characters and amounts above this quantity do not enhance the effects, whereas less than the required minimum does not promote partial development of the characters, whether they be anatomical or functional. This fact was later stated by Pézard as the "all-or-none" law of the action of the sex hormone on the sex characters.

Morgan (50) in 1919 published a most interesting article on the genetic and operative evidence relating to the determination of the sexual characters. In this article he included incidental observations on behavior. He quoted with approval the statement of Goodale to the effect that the capon does sometimes respond with characteristic male behavior in a sexually stimulating situation. From his own observations he deduced that castrated Sebright and other capons treaded hens.

The foregoing authors typify opposing views regarding the effects of castration in the fowl. Pézard (52), representing one view, contends that castration produces a "neuter" or negative animal as regards behavior; whereas Goodale (34) and Morgan (50) contend that sex behavior may occur, but rarely, and only with special provocation, in the capon from which all gonadal tissue has been removed.

The year following Morgan's work mentioned above, Masaglia (48) published evidence supporting the theories of Bouin and Ancel regarding the function of the interstitial cells and their effects on the secondary sex characters and activity. He proposed that a diminution of the cells of Leydig was followed by a decrease in sexual activity. Such a suggestion, when further developed, points to a high degree of correlation between the amount of interstitial cells and the

amount of sex activity. In one of Massaglia's cockerels, from which the gonads had been almost completely removed, no sex behavior was revealed by the techniques of observations employed. In the small piece of tissue remaining a marked decrease in the number of Leydig cells relative to the amount of seminiferous tubules was noted. Massaglia infers that there is a causal connection between the lack of sexual behavior and the fewness of Leydig cells.

At this point, the work of Kuntz (43) is pertinent. This investigator severed the sympathetic nervous supply of testes in the dog and concluded that the operation produced a hyperplasia of the interstitial cells. With this hyperplasia there was an increased sexual excitability. The work is a good example of conclusions that are sometimes drawn regarding the *amount* of sexual drive. His statements are not supported by adequate evidence. That the dog had a heightened sexual excitability very probably was inferred by Kuntz from general impressions and not from adequate test situations. Conclusions so drawn cannot be considered valid. Objective and carefully devised test situations are necessary for the ascertainment of the amount of sexual motivation.

Pézarid (55) gave expression to his concept of the "differential threshold" as applied to the amounts of hormone necessary for the normal development of the different secondary sex characters and behavior. This point of view has been adopted by many workers, but absolute proof of its validity has not been forthcoming.

Hartman and Hamilton (41) in 1922 published second-hand information on the behavior of a case of sex reversal in a female fowl. The bird apparently developed into a normal pullet, but when it was one year old its comb enlarged, its voice deepened, and its vocal pattern of crowing resembled closely that of a genuine cock. Although it was never seen to tread hens it would call them to food. It never fought with normal cocks; nevertheless, it was sometimes attacked by them. During the four succeeding years the individual functioned as a normal hen and adopted a brood of chicks, but it was never seen to sit on the nest. Occasionally it laid an abnormally shaped egg. Histological examinations showed both spermatozoa and oocytes in the left ovo-testis, and the right gonad was found to be a mature testis from which interstitial cells were absent.

A short time later, Gatenby and Brambell (30) published studies on the gonads of fowls. One of their experimental birds, supposedly a female, behaved toward other hens in calling them to food exactly as a male, but "when the unsuspecting hens approached, the abnormal bird did not try to tread but violently attacked them." The individual

crowed. Anatomical examinations showed degenerate nodules of testicular and ovarian tissues. The authors summarized the effects of gonadectomy as follows:

1. Few changes are produced in feathering.
2. Castrated birds seldom crow.
3. Spurs are hardly altered.
4. The capon is not pugnacious and "does not court hens, but if one squats" he will mount and go through the mating reaction.
5. The comb of a capon is extremely small.

The operative techniques of gonadectomy either in the male or the female, as they are usually employed, are always unreliable in the completeness of the removal of all the gonadal tissue. In the process of the operation there is also very great danger of autotransplantation. Hence, the paper by Riddle (58) in 1924 on pigeons congenitally without gonads was particularly interesting to the writer. There were sixteen of these birds "without a visible trace of gonadal tissue," some of which were observed by Charles Otis Whitman and others by Riddle himself. Concerning the behavior Riddle writes: "thorough-going male behavior and masculine desire was strongly exhibited by 'individuals' which were, according to all the evidence, entirely without interstitial and gametogenic tissue" (p. 212). Further he continues: "The repeated observation of exclusive and emphatic masculine behavior in this type of bird seem to make it certain that these expressions of maleness do not here rest upon an internal secretion of the testis—neither of interstitial nor of reproductive testis" (p. 242). Riddle explained the normality of behavior by saying that the functions pertaining to the sexual activity normally taken over by the gonads were subserved in these cases by other structures of the organism. Riddle contends that the situation is different when the gonads have already been *invested with the function of maintaining sexuality*, and when the organs are then "brusky" removed. The above concepts, in his opinion, explain the discrepancy between the generally understood results of castration and the behavior of birds he observed with the gonads congenitally absent. The primary sexual glands, Riddle would say, are not determiners of secondary sexual characters, but the gonads themselves are determined by the zygotic constitution of the organism, and that a differential metabolic rate is essentially fundamental to sexual differentiation.

Finlay (26) in his excellent studies of sexual differentiation in the fowl, made some interesting incidental observations on the

behavior of his birds. Regarding one of the males which had been completely castrated and into the peritoneal cavity of which ovarian tissue had been engrafted, Finlay wrote that it was *reported to him* that the bird did occasionally tread hens but that it also had some of the characteristics of a female. Its behavior seemed not to be asexual but rather intersexual. The necropsy showed a small mass of ovarian tissue but no testicular tissue. Finlay made an interesting comment on the stance of another subject to the effect that "he had not the sex pride which impels the normal male to assume an upright and commanding position" (p. 447). In his partially castrated subjects he found sex behavior, as indicated by treading, when the nodules of tissue were more than one-eighth of the normal amount of the two testes. He gave the following account of one partially castrated bird that retained 2.7 grams of testicular tissue: ". . . the fact that its spurs were not worn, and that it did not fight or exhibit marked sexual instincts, showed that it was incompletely sexed" (p. 447). Birds with undisturbed ovaries and with testicular grafts in the peritoneal cavities showed the sexual instincts normally associated with the intact primary sex organ. Likewise, males with entire testicles but carrying ovarian grafts showed male behavior. In both cases, however, there was modification of the comb, thus showing some effect from the grafts. In summary Finlay writes: "There can be no doubt that there was a fundamental psychological difference between the sexes. The male with ovary grafts still had the mentality and temperament of the male; while the female with testis grafts still had female instincts. The psychological state was of course modified to a certain extent by gonad activity; but it was impossible to develop the mental qualities of a male in a female or *vice versa*" (p. 458). In general he contended that some sexual characters could be modified by the gonads but that the more fundamental attributes of behavior do not follow the gonadal type in the transplantation experiments.

Contrasting to a certain extent with the work of Finlay was the 1926 paper by Pézard (56). In this publication Pézard said that the capon is a mild, quiet animal without the fierce attitude or the proud carriage of a normal cock. He not only will not tread hens but other cocks will tread him as they would a hen. The castration of a pheasant produced an animal which was passive and demure, remained indifferent to females, and never became sexually excited. The normal qualities of male behavior may be restored in the "neuter" animal by grafts of gonadal tissue. Thus it is shown that psychosexual behavior is intimately connected with the gonads.

Caridroit (12), following his extensive experiments of transplanting ovarian and testicular tissues, concluded that the male and female gonads condition respectively the masculine and feminine instincts, although cocks with ovarian grafts have to a greater or less degree shown qualified male instincts. Caridroit contended that there is an antagonism between the effects of the two glands in their potentialities for conditioning the male and female instincts. Castration in the Sebright bantam, he found, caused a loss of the sex instinct. An attempt to graft ovarian tissue in ovariectomized females resulted in the successful implantation of sufficient tissue to maintain the "sexual instincts and song." Caridroit concurs with Pézard in the belief that the different secondary sex characters have "differential thresholds" of amounts of necessary hormone. It appears that Caridroit was attempting to duplicate the experiments of Steinach (65) involving complete operative sex reversal, but it is evident from the article that the two sets of results are not highly compatible.

Roxas (62) in his investigation of the effects of cross-transplantation of the Leghorn and Sebright testes, suggested the hypothesis that the head furnishings and instincts seemed to depend on the autocoid of the testis, while the plumage was conditioned by additional genetic factors.

Rowan's (60) article, published in 1926, touched on the subject of the effects of the gonads in migratory birds. "It seems unlikely," he said, "from evidence at present available, that moults are dependent on the gonadic hormone as a stimulus" (p. 169). He concluded that the migratory impulse seemed to be synchronized with the breeding impulse, although he did not connect the two phenomena causally or postulate a common source of motivation. It is hoped that Rowan will soon use the technique of gonadectomy in his experiments on the migration of birds, in order to find out how much of the motivation to migrate is derived from the primary sex organs.

Zawadowsky (72), on the basis of results obtained from normal and incompletely ovariectomized hens bearing testis grafts, came to the conclusion that the behavior remained that of a normal hen but if the ovary is underdeveloped or becomes atrophic, the testicular grafts may dominate the sexuality of the internal environment; then the instincts will be those of a cock. On this theory the maleness or femaleness of the organism will depend on the relative quantities of male or female sex hormone in the blood stream. Logically it would be possible to have the factors equally balanced, and hence a neuter organism would result with abundant hormones of both sexes.

Until this condition is developed experimentally the theory of antagonism between the male and female hormones will remain hypothetical.

Domm (24), in a publication of the results of his excellent work on the effects of ovariectomy on the somatic secondary sex characters in female fowls, writes as follows: "It seems to be relatively well established that the gonadless male is comparatively neutral in its behavioristic reactions. Our evidence leads us to believe that such an individual neither crows, treads, nor fights; in general, he exhibits none of the normal male reactions" (p. 116). The ovariectomized hen, while in the capon-like condition before the development of the right ovo-testis, is never heard to cackle or sing like the normal female. After the ovo-testis on the right side has developed, many birds carrying such a structure crow regularly; however, their voices seem to be shriller than those of the males. A number of these birds are known to sing but can be distinguished from females by their coarser voices. Domm says that "The reactions of the poulard while in the capon-like condition are very similar to those observed above for the normal capon. She seems even more shy in her behavior. I have never observed her fighting with a cock. . . . The poulard developing head furnishings of the male has a widely different disposition. . . . Such an individual will fight with every bird put in the pen, not infrequently assuming the initiative. Even when introduced into a pen with a normal cock, such a bird will be found to fight" (p. 89).

With respect to capons Domm writes: "It is generally conceded that the capon does not fight cocks, that he shows no interest in the hen and does not tread. The capon thus loses the psychosexual behavior of the cock. Our observations agree in general with this characterization. Notwithstanding, we have capons in our pens which are pugnacious, fighting every cock introduced. These birds crow and tread other hens, having most of the characteristic reactions of the normal male, but in a milder form" (p. 89). He continued to say, however, that these animals upon necropsy usually showed small nodules of testicular tissue with the characteristic tubular formation, and that they showed normal spermatogenesis. The important results of Domm's experiments are: (1) There is a masculinization of the ovariectomized female fowl which is concomitant hyperplasia and development of the right rudimentary ovary. This organ, when it has grown, has a characteristic seminiferous tubular formation; Domm, however, has not found active spermatogenesis as have some of the foreign workers. (2) Just after the removal of the functional

ovary of the female fowl and before the development of the right rudimentary ovary there is a period when the operated animal behaves as a capon.

Lillie (44), in the summary of his article on sex-reversal of the female fowl, formulated an hypothesis which accords with the concepts of Zawadowsky. The hypothesis is that the central nervous system retains the capacity to react in one of two fixed ways (genetically determined), *i.e.*, in a masculine or a feminine manner, to the "induction" influence of the sex hormones. Earlier in the article Lillie says, "Certain parts of the organism retain alternative potencies throughout life; the nervous system is presumably such a system par excellence." In this last connection Lillie was referring to the reactions of the nervous system to experience and training. From his article comes the thought that the nervous system is not only modified by external influences but that a profound part of its development comes from within and from genetic potentialities.

In 1927 Greenwood and Crew (38) described eleven male fowls which throughout their lives retained all characteristics of individuals completely castrated before puberty with the exception of the comb, which although diminutive in size, was bright red in color. Post-mortem examinations revealed that the gonads either were absent or greatly reduced in size and that the *spermatogenic processes* were imperfect. Crew (19) in his description of a case of sex-reversal said: "the crow became challenging and the disposition bellicose toward cocks, courteously masterful toward hens. The bird treads hens and fights cocks" (p. 257). Further he wrote in describing another case, that the bird fought with any and every male in the yard and was courteous towards hens. Cases of sex-reversal, according to Crew, behave typically by fighting males and courting hens. Crew stated that it was unknown in many cases of sex-reversal whether the imperfection was in the primary sex organs, in the soma of the animal genetically, or otherwise determined.

Interesting observations on the voice were made by Michalowsky (49) in 1927. This worker noted, following the injection of $ZnCl_2$ into the testes, which compound caused a degeneration of the germinal epithelium and an hyperplasia of the interstitial cells, that the birds so treated did not crow and exhibited few evidences either anatomically or behavioristically of a male. Nevertheless, the process of spermatogenesis was noted in the injected animals.

Perhaps the most serious attempt up to 1928 to investigate voice changes following modification of the male and female sex organs was that of Appel (2). After a careful study of the gross and histo-

logical aspects of the syrinx he concluded as follows: "No sexual dimorphism has become apparent in the syrinx of the Brown Leghorn fowl, and there is no modification of the syrinx following ovariectomy or castration" (p. 512). He wrote further: "There is no apparent reason why the female (Brown Leghorn) fowl should not crow provided it had the instinct to do so properly developed." According to Lillie (44), the sex hormone, if it acts in voice production, must act entirely through the conditioning of the central nervous system. There seems to be great individual variation in the syrinx of the fowl but these variations do not correlate with sex factors, according to Appel.

The present writer would question the conclusiveness of Appel's findings. It is possible that the results of his technique of study were interpreted correctly, but one may well be doubtful whether differences in the functional capacity can be detected by the histological procedure employed. Small differences in *muscular tension*, a functional quality, may and do produce differences in vocal qualities, and these minute variations in function are probably not indicated by histological techniques which bring out structural details. It is suggested by the present author that the differences must be in part produced by variations in the structural development of the vocal mechanism, but that mainly the causes for varying vocal qualities in birds with modified primary sex organs lie in the reactivity of the functional *neuromuscular vocal mechanism* to the sex hormone. A greater refinement of technique may reveal the facts more accurately.

Some important data on the turkey have been collected by Athias (4) who first reported in 1927 and subsequently gave a second report to the London Sex Conference in 1930 (5). When castration is performed on animals in the prepuberal stages of development, strutting, which seems to be a sexual activity corresponding to charging and display in pigeons, only rarely occurred. The castrated male would brood young, a feminine modality of behavior in this genus, but the normal male activities associated with and including copulation were not displayed.

Lipschütz and Wilhelm (46) performed experiments of gonadectomy, the results of which were published after the experiments of Carpenter (16) had begun. They used six animals and castrated them to determine the effect on feather growth and development. Of the six pigeons, four did not mate, but the two that mated showed normal behavior in the cycles of reproduction. The authors reported that the psychosexual behavior of these birds was negative, and that it was possible for the laboratory boy, who made the observations and

detailed the information to the writers, to separate the birds by observing their behavior and without help of the protocols of the operations. Three of the birds did not participate in nesting activity or feeding of the young as is characteristic of the normal male pigeon. Post-mortem examinations revealed that of the four animals that did not mate, three of them carried no gonadal tissue while the fourth carried a nodule of tissue weighing 14 mg. The two animals with normal behavior carried about 90 mg. each of gonadal tissue. Lipschütz and Wilhelm conclude that some secretion of the gonad does condition the reproductive behavior of the male pigeon. Obviously neither the number of animals nor the technique employed by the foregoing workers was adequate for the establishment of detailed, accurate information regarding the effects of castration on the reproductive activities of the pigeon.

The most complete review of the literature and the most intensive investigation of the primary sex organs in fowls was published by Benoit (7) in 1929. In this article of two hundred and eighty-two pages, in which were made detailed citations on sex-reversal and on the effects of castration, X-ray exposures, injections, and grafts, upon the somatic secondary sex characters, approximately two and one-half pages only were devoted to the alteration or changes of behavior following these operations. Benoit wrote that he had seen capons tread hens but that such behavior was the exception rather than the rule. He overlooked the fact that no variations occur without a cause. Benoit reported one test situation arranged for his subject D53. He demonstrated that the animal could copulate; however, this occurred at the end of some minutes. The bird had the typical capon head furnishings, and a rigorous necropsy failed to reveal any testicular tissue. It was the opinion of Benoit that the capon usually did not seek the hen because the capon was "deprived of the male sex instinct." In his consideration of pugnacity Benoit added:

The fighting characteristic of the cock is equally suppressed by castration. The capon does not have the quarrelsome instincts. He becomes very calm and gentle and slow; he moves little and rests willingly. Some exceptions to this apathy have been indicated. Sellheim refused to recognize the cowardice and indolence of the capon. Some animals that had been castrated for a year showed the fighting instinct. They would fight among themselves and with normal cocks. I have myself sometimes noted in my laboratory that if capons were provoked by cocks, they would pursue them and, ruffling their feathers, they would engage them in a brief fight. (Trans., p. 375.)

Carpenter (16) in 1931 completed an intensive study of the effect of partial and complete gonadectomy in the male pigeon. The *time-limited systematic observational technique* was used to measure the strength of the sex drive. This method yielded two types of scores: the provocative scores, or the time from the beginning of a test situation until the occurrence of the first copulation, and the frequency score, which was the number of copulations enacted during a definite period of time under optimum conditions for the occurrence of the behavior under scrutiny. Systematic tests for fighting were made also. The techniques used had sufficient reliability for group differentiation. Forty-six operated and twenty-eight normal birds were used in the investigation.

Birds were operated at thirty, ninety, and one hundred and fifty days of age. Also there was a heterogeneous group of adults which were five years of age or older. The data made possible the construction of curves which showed a decline in the sexual activity following postpubertal castration. In some of the cases this score almost reached zero. Curves drawn from the data on the birds that were operated prepubertally, *i.e.*, before they had been allowed opportunity for any sex experience, showed that there was a lack of normal development. Of the complete operates, most of the birds that were castrated at thirty days of age showed a small amount of sexual activity, but a few obtained zero scores during nine series of seven tests each.

An analysis of the behavior in normal birds and in the operates was made both by observational and by moving picture techniques. Primary and secondary sexual activity and the other reproductive modalities of behavior of nest building, brooding, and feeding of the young were studied. The following conclusions pertinent to this review are drawn from this study: (1) The form of the copulatory act, when it occurred, was not essentially changed by castration, except that it became somewhat slower in the initial stages, but the frequency of coition in the completely and incompletely gonadectomized birds ranged from zero to normal. There was an increase in the average duration of the time from the beginning of the test period until the occurrence of the first copulation (provocative scores). (2) The frequency of billing and charging, secondary sex activities, in the complete and partial castrates ranged from zero to normal. The mean provocative scores were also increased in the operates. Also, the mean provocative scores for billing were increased in the operates. The patterns of action were not changed essentially. Of the secondary sex activities, preening was least

affected by castration. There was a high correlation ($+0.74 \pm .001$) in the normal birds between the secondary sex activity of billing and copulation as measured by the frequency scores. (3) Complete and partial castration greatly reduced the duration of nesting activity and increased the period of provocation for this behavior in the male pigeon. (4) Complete and partial castration of the males of mated pairs of pigeons caused a reduction in the nesting activity of the associated females which corresponded closely to the degree of reduction in that type of behavior in the male. (5) Brooding behavior in the male pigeon is the first of the modalities affected after complete and partial castration of mature and mated birds. (6) Partially castrated birds tested for feeding of the young behaved normally. (7) General activity, as scored by a carefully devised, systematically carried out rating scheme, was greatly reduced by complete castration at each age, and affected in varying degrees by partial castration. (8) Fighting behavior was considerably reduced but not completely eliminated by complete castration, and was reduced in varying degrees by partial castration. In some individual tests, normal fighting occurred. (9) Vocal expression was slightly, if at all, affected by partial castration of the adult male pigeon. (10) Castration of the immature male pigeon is followed by failure of normal vocal development. It is possible that a greater amount of the sex hormone is required for the maturation of the voice than for the development of some of the other secondary sex attributes.

SUMMARY AND CONCLUSIONS

Slowly through observations and experimentation it has been found that some hormone produced by the testis is fundamental to normal motivation of sexual activity, either directly or indirectly through its effects upon other glands and the nervous system. The review of the literature pertinent to this subject makes the fact clear that work in this field has just begun. Most of the observations on sexual behavior have been incidental to the main purpose of the investigations, namely, the study of secondary sex characters, among which behavior sometimes was classed. The studies bearing specifically on behavior have been few and inadequate. Appel considered the voice with special attention being given to the anatomy of the syrinx. Lipschütz and Wilhelm gave a report of the observations of their laboratory keeper on the behavior of three completely and three incompletely castrated male pigeons and found the completely castrated birds to be inactive sexually. Van Oordt and Bol found that castration had no effects on the "homing" activity of pigeons.

Carpenter employed a somewhat quantitative method in measuring the lack of normal development of sexual behavior in prepuberally castrated male pigeons; also, he measured the decline of sexual behavior in birds gonadectomized as adults. Carpenter studied forty-six operated birds and twenty-eight normal animals as controls and gave attention to the two modalities, reproductive behavior and fighting. Four groups were studied for from six to nine months. He found that the majority of the birds diagnosed as complete operates showed a minimum of sexual behavior of the primary type.

The following investigators have found some primary and secondary sex behavior following gonadectomy: Foges, Morgan, Goodale, Domm, Benoit and Carpenter. Most of the authors agree that when a castrate does engage in any sexual activity there is a supernormal stimulation or provocation. It is evident to the author that sufficient data have not yet been gathered on the question of whether or not a fowl which has *never had the effect* of the gonads, will engage in primary sexual activity. A conclusive opinion, therefore, from the summary of the literature cannot be given.

The information from the articles that have been published pertinent to the subject under consideration lack conclusiveness for the following reasons: (1) Behavior, *per se*, has not been given the emphasis that it deserves in studies on castration and sex-reversals; (2) sufficient animals have not been used to make the findings reliable; (3) adequate techniques for the detection of fine differences in behavior, such as the decline of motivation following castration, have not been employed by most of the investigators; (4) the technique of gonadectomy in many birds, wild migratory birds for example, or even the pigeon, is a rather difficult operation and there is great probability that some tissue may be left intact after the operation and overlooked in the necropsies. These difficulties or points of objection must be kept in mind in evaluating the results of the foregoing publications.

In conclusion, it is necessary to say that before the exact effects of castration can be stated there must be an improvement in the technique of operations. The author suggests repetitive application of a technique employing an aspirator and cauterizer for the final removal of the glandular tissue. The techniques of observation may also be improved. The time-limited systematic observational technique used by Carpenter should be checked and further developed.

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SPECIAL REVIEWS

WARDEN, C. J. *Animal Motivation; Experimental Studies on the Albino Rat*. New York: Columbia University Press, 1931. Pp. xii+502.

This volume as pointed out by the authors in the preface represents the final published report of a "comprehensive experimental investigation of animal motivation" carried on under the direction of Professor Warden in the animal laboratory of the Department of Psychology, and financed by a grant of \$5,000 from the Council for Research in the Social Sciences of Columbia University. Most of the material included in the book has been published previously as separate papers or monographs when the experimental work on the various projects was concluded. The experimental results reported in the main body of the book were obtained by use of the Columbia Obstruction Method of testing motivation. This method consists of placing, between the animal and some form of incentive, an obstruction in the form of an electrified grid giving a standard shock. The strength of drive is measured in terms of the number of times that the animal crosses the obstruction to reach the incentive within a specified interval of time, viz., twenty minutes. The apparatus and the technique for testing the strength of drive were carefully standardized and were then used to study under various conditions and especially to measure the strength (maximum) of five drives: the hunger drive studied by L. H. Warner and by E. L. Hamilton; the thirst drive by L. H. Warner; the sex drive by L. H. Warner, by M. Jenkins and by H. W. Nissen; and the maternal drive and the exploratory drive by H. W. Nissen. Professor Warden has added the general introductory section to the report, an introduction to the discussion on each of the above-mentioned drives, and a concluding section devoted to a comparison of normal drives in terms of their relative strength and persistence in the white rat, a comparison justifiable because the standardization of experimental conditions and techniques made the scores for the various drives directly comparable. As a result of the comparison of group averages the normal drives are ranked in order of strength as follows: maternal, thirst, hunger, sex, exploratory. In an *Appendix* are presented four related studies which were financed from the same grant as the main projects and

which were done under the direction of Professor Warden. One of these, that done by Frances Holden, reports the first study in which the Columbia Obstruction Method, later modified for use in the main projects, was used. The other three studies, two by E. L. Hamilton and one by Mercy Aylesworth, report studies on animal motivation in which techniques other than the Columbia Obstruction Method were used.

The Columbia Obstruction Method is an attempt to develop a *test* method for the study of animal motivation. Professor Warden and his collaborators expended a great deal of effort in standardizing the apparatus and technique and, in the opinion of the reviewer, that aspect of their work constitutes a valuable contribution to the scientific study of animal behavior. In dealing with a test or any type of apparatus, it is equally essential to establish the reliability and validity of the measuring instrument and of the technique. An attempt was made in this direction also but, again in the opinion of the present reviewer, that attempt was not as extensive as it might well have been in view of the considerable amount of work that has been done with the method. In Part I, Section 2, of the book is reported a study by Warden and Nissen the general purpose of which was "to determine how adequately the Obstruction method, as finally standardized for our project, gives a valid measure of drive-incentive behavior in the white rat." This was done by trying to isolate the two most important features of the apparatus by usual experimental methods and to determine the influence of each in the measurement of drive behavior. Both the obstruction and the incentive as tested are shown to be dominating factors in the situation since pronounced differences appear between groups tested with and without the obstruction, and with and without a specific incentive. The effect of retesting on the animal's behavior was also studied but with an experimental group of only eight animals. The rank order for these eight animals on each of nine retests shows but slight variation in the relative position of the individual animals in the retests even though the actual number of crossings as measured by the average for the group steadily increases. Although from the results with this group the test-retest reliability with intervals of three days between tests appears to be high, it is regrettable that retests were not made with larger groups of animals. Since most of the other groups used in the various studies consisted of twenty animals, retests on one or more of those groups, which would have required little additional time, would have given a somewhat more adequate measure of test-retest reliability than could be obtained with only eight animals.

In the discussion of the degrees of standardization of method and procedure (Part VII, Section 1) emphasis is placed on the use in these studies of normal animals from the same strain (Wistar Institute experimental colony strain or first or second generation), of the same age (with certain exceptions noted by the authors) and reared and maintained in conditions kept as constant as possible. Aside from this the implication is that no selection was exercised as far as the animals were concerned. Yet careful reading of the volume brings to light the fact that in at least one of the basic studies of the project an additional factor entered into the selection of the experimental animals. In the introduction to Dr. Warner's study on the sex drive the following statement appears (p. 119): "The general purpose of this investigation was the study of the sex behavior of the *normal** male and female albino rat." On page 143 Dr. Warner in a distribution table covering the number of matings during the two hour period prior to the segregation of his male rats indicates that no male rat in his group of 160 refused to copulate during this two hour period. On page 192 in a similar distribution table covering the number of matings during a similar two hour period prior to segregation, Dr. Jenkins shows that 58 of the 79 male rats used by her did not copulate during the two hour period. The latter author attempting to account for the disparity between these results obtained from groups sufficiently large that one might expect more similar distributions, points out that weather conditions may have been responsible for this difference and then continues (p. 193), "A second explanation should be considered. Dr. Warner has privately informed the writer that he only tested males which copulated on the ground that only males which copulate are normal." This use of the term "normal" is in a sense somewhat different from that usual in psychological literature and consequently implies the introduction of a selective factor not mentioned in connection with Dr. Warner's study except in the quotation from Dr. Jenkins. Nevertheless the results from Dr. Warner's study are used again and again as measures of the sex drive in the normal male and compared with results from other studies in which no such selective factor was operative.

It appears to the reviewer that the definition of drive by Dr. Warden as ". . . an aroused reaction tendency which is characterized primarily by the fact that the activity of the organism is directed toward or away from some *specific incentive* . . ." makes essential, before a valid comparison of the relative strength of different

* Italics mine.

drives be attempted, demonstration that the obstruction method gives an adequate sample of the drive involved. As far as the reviewer has been able to discover no attempt has been made to determine whether the Columbia Obstruction Method gives an adequate measure of the strength of drive or whether it measures only certain phases of the incentive-drive behavior. Some observations are reported which raise some question as to the adequacy of the method. Dr. Warner in discussing the results obtained with the eight-day group in his study of the hunger drive says, "In spite of their weakness these animals showed a definite orientation toward the incentive compartment. This is indicated by the fact that although they crossed less frequently than did the animals of the six-day group they approached and made contact without crossing even more frequently. After observing the behavior of these animals one is tempted to say that the hunger drive is as strong as ever and that reduction in crossings is due to decreased capacity to resist the shock. Starvation may possibly effect not only the animal's tendency to approach food but its capacity to undergo electrical stimulation" (p. 70).

It has already been pointed out (Leuba, C. J., Some Comments on the First Reports of the Columbia Study of Animal Drives, *Jour. Comp. Psych.*, 1931, 11, 275-279) that the relative strength of drives present in the various drive situations used as given in terms of group averages are a function of the length of the experimental period and that if periods of greater length than that used, viz., twenty minutes, had been used the results as shown by the detailed statement of the data would have given the various drives different relative positions. This, to the present reviewer, appears as a justifiable criticism of the work reported in this volume. For further discussion of this point see the reference given above.

On the other hand, in justice to the book it must be said that its merits outweigh its defects. It represents a very important contribution to the study of animal behavior because of the careful standardization of the apparatus and technique, because of its systematic attack upon a relatively unexplored field and because of its comprehensive character.

W. G. McALLISTER.

University of Illinois.

KEELER, CLYDE E. *The Laboratory Mouse*. Howard University Press, 1931. Pp. 81.

This is an instructive little book which deals with the origin, heredity, and culture of the mouse. The topic headings are:

I. Introduction; II. Geographical distribution of the house mouse; III. Antiquity of the fancy mouse; IV. Unit-characters (gene mutations) of the house mouse; V. Normal inheritance; VI. Abnormal inheritance; and VII. The breeding of mice in laboratories.

The book concludes with a series of plates showing a number of varieties of the mouse and several abnormalities. There is also a bibliography of 184 titles.

Because of the close relationship of the mouse and rat this book will, no doubt, be of interest to a great number of animal psychologists as well as to those investigators who deal more specifically with the mouse.

W. T. HERON.

University of Minnesota.

BRETEGNIER, L. *L'activité psychique chez les animaux*. Paris: Vigot Freres, 1930. Pp. xi+387.

This book has a subtitle, *Instinct and Intelligence*. It is written in an easy, popular style. The first chapter deals with the historical aspects of the question. The author starts with the Ancients and comes up to the present, giving the opinions of literary men, physiologists, biologists, naturalists, psychologists, moralists, and others all in one array concerning the mind of the animal.

In the second chapter he discusses the various methods of studying the psychology of the animal. He includes some of the representative methods familiar to animal psychologists although he does not mention any of the recent refinements of these methods.

The various chapters proceed with the discussion of tropisms, reflexes, instinct, the psychic characteristics of the social insects, the affective states in animals, intelligence in animals, and language in the animals.

While experimental material is not overlooked in the discussion of these various topics, still it seems to the reviewer that the author has inclined rather heavily towards the writings of those who use predominantly the naturalistic approach to the problems of animal psychology. Therefore, while much of the material in the book is very interesting and instructive, it is questionable whether the author has produced a work which completely conforms to the standard accepted for a scientific treatise.

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